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BY
B. E. QUICK

A DISSERTATION SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMENT FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN THE UNIVERSITY OF MICHIGAN

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# A COMPARATIVE STUDY OF THE DISTRIBUTION OF THE CLIMAX ASSOCIATION IN SOUTHERN MICHIGAN

B. E. QUICK

## I. Introduction

During the 1911 season of the University of Michigan Biological Station on Douglas Lake in Cheboygan County, Michigan, many differences were noted between the beech and maple forests of this region and those of the southern part of the State. The presence of different species of dominant trees in these woods as compared with those farther south, as well as the differences in the herbaceous vegetation, suggested the advisability of making comparative studies of beech and maple woods throughout the Lower Peninsula of Michigan in order to determine whether the differences were sufficient to classify as distinct types these forests which had possibly entered the State by different routes, or whether they might be part of the same vegetative type differing merely in certain climatically limited species. The soil requirements seemed also of interest, as this kind of forest occurs in the north on light soils, while in the south, especially near Ann Arbor, it is found on heavier soils.

During the academic year of 1912–1913 and the summers of 1912, 1913, and 1914 investigations were made under the direction of Dr. H. A. Gleason, of the University of Michigan. To him I am indebted for his kindly interest and many valuable suggestions, as well as for access to some notes taken in travelling about the State. I am also indebted to Professor F. C. Newcombe for many useful suggestions and criticisms.

Species lists, habitat and soil notes, as regards not only the original condition, but also the degree of modification of the

same by plant growth and counts of the trees present for percentage of abundance of the dominant plants were made for all of the stations studied; quadrat studies were made in many cases also. Notes made from trains in going from one part of the State to another were found, when verified by data taken on foot over the same areas, to be of value in studying the soil preferences as well as the general distribution of many of the larger species of plants.

The nomenclature used throughout is that of the seventh edition of Gray's *Manual of Botany*, so no other authorities will need to be cited for the individual plant names. The herbarium at Michigan Agricultural College, as well as the one at Ann Arbor, was consulted in reference to the identity and distribution of several plant species.

The illustrations are all from photographs made, developed and printed by the author.

## II. General Considerations

### A. CLIMATE

The climatic character of the southern part of Michigan can well be expressed by the following figures. The three cities selected for the graphs in Figures 4 and 5 were chosen because they showed extreme variation in the climatic factors, and also because they were located at wide distances from one another. Alpena is located on Lake Huron near the northern end of the peninsula; Port Huron is on the same side of the State, but farther south, below the "Thumb" region, while St. Joseph is on Lake Michigan near the southwest corner of the State. The data used in the curves were gathered from the United States Weather Bureau report for 1912, and represent the averages of twenty to thirty years of observation. The mean temperatures vary similarly in the three places; the mean temperature for the entire Lower Peninsula is close to that for Port Huron. The maximum and minimum temperatures are strikingly close together in range and in values, both being less extreme than those given for northern Illinois by Gleason (1910). Mean tempera-

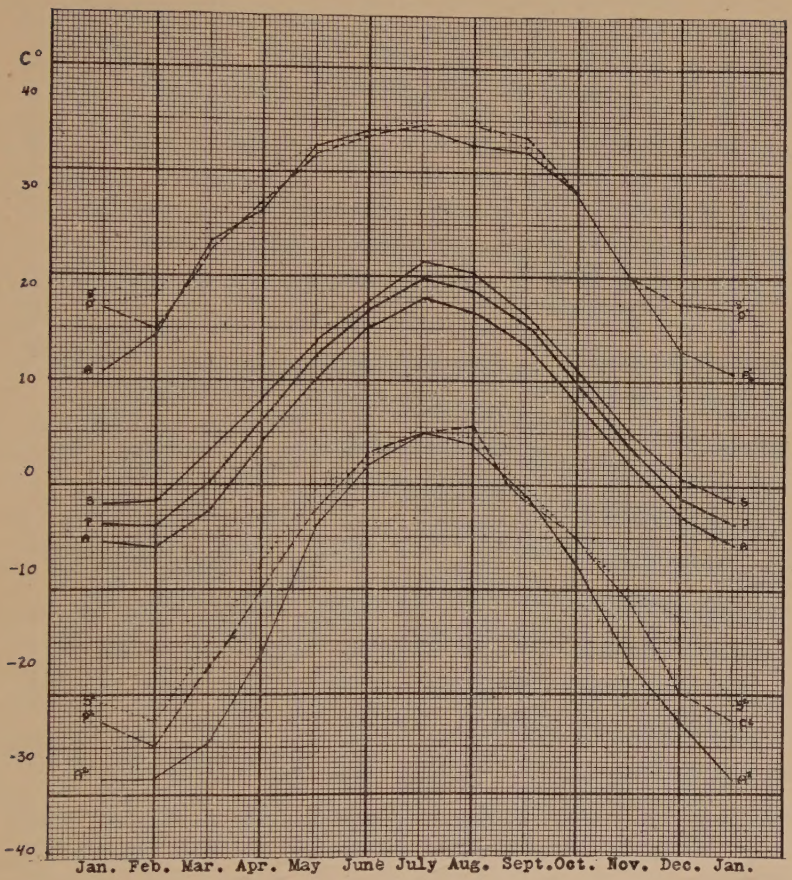



FIG. 4. Temperature Curves for Alpena, Port Huron and St. Joseph. A, P and S, mean temperatures from January to January; A′, P′ and S′, maxima; $A^2$, $P^2$, and $S^2$, minima.

Constructed from records published in U.S. Dept. Agric. Weather Bureau Bull., sections 62 and 63, 1907.

tures seem related to latitude; maxima, to neither latitude nor the nearness of the lakes; minima, to latitude, but in a very irregular manner.

For the Lower Peninsula the average latest killing spring

frost occurs about May 10, and the earliest in the fall about October 4, so the growing season averages about 140 days. Alpena has an average growing season of 135 days, Port Huron of 154 days, and St. Joseph of 177 days. The length of the growing season is generally dependent on the latitude, but is also influenced by the nearness of the Great Lakes, especially Lake Michigan. The winds come from a generally western direction, and, sweeping across this lake, they give up in summer or take up in winter a considerable amount of heat, which greatly moderates their effect. This is best demonstrated by the

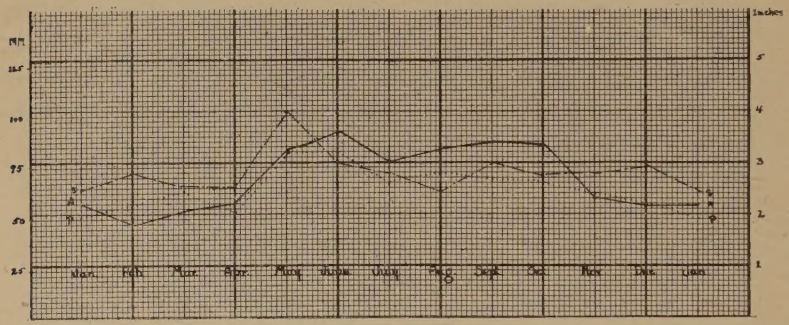


FIG. 5. Chart of Rainfall. Expressed in millimeters to the left and in inches to the right. A = Alpena, P = Port Huron, S = St. Joseph.

Constructed from records published in U.S. Dept. Agric. Weather Bureau Bull., sections 62 and 63, 1907.

results in an area of moderate temperatures called the "fruit belt," which lies along the western side of the State parallel to the lake.

Past students of the climatic conditions have divided this region into different climatic zones. Transeau (1905) mapped areas of "relation of rainfall to evaporation," three of which entered the Lower Peninsula of Michigan. Livingston (1911) divided the State into three zones, at right angles to Transeau's, in mapping areas of like evaporation, and later (Livingston and Livingston, 1913) made maps of temperature summations and also of "temperature efficiencies," in both of which the zones resembled those of Transeau in a general way. As was shown

by Brockmann-Jerosch (1913), single characters of any sort are insufficient for demarking plant zones; and, in general, meteorological conditions are of little value in explaining differences in vegetation for the smaller regions, although they may be significant for the larger ones.

### B. GEOLOGICAL HISTORY

The geological history of Michigan is of interest in two ways: first, because it determined the nature of the soils, and, second, because it directly controlled the time of entry, as well as the order and place of entry of the present flora.

At the time of the glacial period some 15,000 to 50,000 years ago, the great ice-sheet covered Michigan and extended as far south as the valley of the Ohio River. After several retreats and re-advances, the final retreat of the ice left the State with its former rock masses planed down, its former valleys filled, and its surface covered with a general mantle of rock-débris and drift which varied in thickness. The soils thus derived are various in character, as well as in origin: some are clays, sands, or gravels left as moraines by the gradual melting of nearly stable ice-margins; some are deposits in the beds of glacial streams with variations in coarseness depending on the rate of flow in the streams at the time of deposition; still others are fine sands or gravels laid down in ancient lake-beds.

### C. ORIGIN OF THE FLORA

During the farthest advance of the ice-sheet the entire State was covered with a deep layer of ice, so that all previous vegetation was completely destroyed. These ice-masses persisted for a long enough time to sterilize the soil completely, at least as regards the higher plants, so that on the retreat of the ice no plants or plant parts remained alive, and large areas of bare soil were left exposed. Geological studies have shown that the ice-margin was not that of a single sheet, but that several retreats and re-advances were separated by periods of temperate

climate which left vestiges in the form of plant remains between the layers of glacial soil. Following the last retreat of the ice, boreal plants occupied the soils growing close to the ice-margins on the higher areas not submerged in the glacial lakes as tundras and bog-associations.[1] Then came conifers on the east and west, and finally deciduous trees advanced from the south to replace the conifers. The conifers were not present in the Ohio Valley, so that the deciduous trees and shrubs directly replaced the tundra and bog-associations in the south central part of the State (Transeau, 1903).

While deciduous forests entered from the southeast, prairies entered from the southwest, being later almost entirely replaced by the deciduous trees. The advances of forest and prairie were not simultaneous, but they alternated in waves, due either to alternating moist and dry periods, as was shown for Scandinavia by Blytt (1881), or to warm and cold periods (Hay, 1910), which would bring about the same effect by increasing or decreasing the evaporation with unchanged precipitation. The general tendency today seems toward a more moist climate (Knowlton, 1910), and this is shown by the present advance of forest on prairie as well as by the advance of deciduous forest upon coniferous forest.

## D. THE UNITS OF VEGETATION

### *The Formation*

Although plants have been discussed from the time of Humboldt in regard to their relations to one another in the natural groupings in which they are found, there has always been some disagreement as to the names for these natural groups. The larger divisions of vegetation were given a name in 1838 by Grisebach (Warming, 1909) when he spoke of a "formation" as "a group of plants which have a decided physiognomic character, as a meadow, forest, etc." A recent use of the term formation is that of Nichols (1917), who defines it as "an asso-

[1] Adams, 1902; 1905 B; Cowles, 1911; Harshberger, 1904 A, 1905; and Scharff, 1912.

ciation-complex which is related to a specific physiographic unit area," in which the "association-complex" includes the idea of a successive series of plant groups, quite possibly of different physiognomic character. It is more in keeping with the original idea of the term to define it as follows: A *formation* is a group of plants of the same physiognomic character which dominates a large region or province as its characteristic vegetation. An example of this would be the *deciduous forest formation* which dominates the Northeastern Deciduous Forest Province, and would include all of the deciduous forests of the region, whether they have or have not successional relations to one another.

### *The Association*

The association is a more restricted group of plants, subordinate to the formation. Humboldt first used this term in 1807 (Warming, *l.c.*). Warming calls the association "a floristic species of a formation which is an oecological genus." Nichols (1917) defines it as "any group or community of plants which occupies a common habitat" and also "any stage in a given successional series." In this paper the term *association* will be used as a natural group of plants whose interrelations and individual peculiarities enable them to live together as a homogeneous community of definite biotic composition. The definiteness of the habitat has been disregarded here, for the character of the association depends more on the forms associated together in it, and on how they associate, than upon the environment where it happens to have developed.

In any association certain forms dominate either by their size, abundance, or effect on the environment, and so are called *dominants*. These dominants may be either a single species or several species in any association, and in the latter case may be present in different proportions in the different *consocies* (Gleason, *l.c.*) of the association. Certain dominants are usually common to two or more such consocies, and the secondary plants are often entirely the same; in other cases the dominants will be alike and the variation will occur in the secondary plants. An

association is thus seen to be a variable, and to vary about a mean in the same way that a species does.

### *The Climax Association*

Besides the fluctuating changes in the association mentioned above, the association is also constantly changing in a definite direction. Each association changes the conditions of light, soil and water for the habitat which it occupies, and these changes make possible the entry of plants able to endure the changed conditions. The entry of these invaders may mean the replacement of the pioneer association, especially if the seedlings of the pioneers are intolerant of shade. Such successions occur repeatedly until an association develops which is not merely able to endure conditions as it finds them, but to perpetuate these conditions, and so live undisturbed unless the balance is upset by climatic change, or by destruction by a cataclysm. Such an end member of a series of successive associations is called a *climax association.*

Whatever the nature of the initial conditions in a region, whether hydrophytic or xerophytic, there is a modification of them in a mesophytic direction. When the conditions are finally established, the vegetation has also arrived at the corresponding condition, and we have the climax association occupying the region in all of its thoroughly matured areas. The nature of the climax association is therefore mesophytic (Fuller, 1914).

For any of the provinces of North America so far delimited, there does not seem to be a definite climax association, i.e., one which can be called the climax for the entire province; there is, however, a tendency in that direction. For smaller areas the climax can often be positively identified, or even predicted from comparisons with similar areas. When two provinces are in contact, there is a struggle for supremacy between the various associations of both, and the climax will be now that of one province, now that of the other, depending on the conditions of soil, water, and topography. It is readily seen that with base-leveling, humus formation, and the consequent increasing mesophytism of the environments, the more

mesophytic climax association will ultimately survive in such a region. Thus there is an advance of one province upon the other, so we may be able to predict a *climax formation* which will ultimately dominate all of the land surface as far as climatic conditions will allow.

In the deciduous forest province of North America the dominant formation is deciduous forest, and all of the associations of this province are tending toward a certain formation which is represented in the smaller areas by the several higher members of the successions. These will be seen to be most similar when we examine the climax associations. One of the most noticeable features of the climax associations described for different parts of this province is the occurrence of Fagus in all of them, with a changing array of other species. The predominance of the beech is noticeable, however, only in the more northern localities and in the Alleghenies. Fagus has been listed in the climax associations of Alabama by Harper (1914), in North Carolina by Harshberger (1903), in Maryland by Shreve (1910), in Kentucky by Evans (1889), and in Pennsylvania by Harshberger (1904 B). In more northern regions it has been given a prominent place in the climax association as one of the dominant species. This has been shown by Roberts (1914) in Massachusetts, Nichols (1913) in Connecticut, Kearney (1900) in the Appalachians, and Bruncken (1902) in Wisconsin, as well as in Michigan (*vid. seq.*). There is an increase in the importance of Fagus as regards the climax association as one leaves the southern part of the province and approaches the contact with the northeastern conifer province.

## III. Studies of the Climax Association in Michigan

### A. historical

The Lower Peninsula of Michigan lies in the edge of the deciduous forest province, and is also occupied by the southern border of the northeastern conifer province, besides receiving the outposts of the prairie province in its southwestern corner.

These facts are responsible for the great variety of associations present, and the successional relationships are often much involved in consequence. This may explain why these successional relations have been neglected by so many of the botanists who have described the vegetation of the State. Cowles (1899) described the climax for fixed dunes near Lake Michigan as a mesophytic beech-maple-hemlock forest in the maple-basswood series. He also described as climax forests coniferous woods alternating with oak woods on less mesophytic dunes. Although these last are apparently stable, they are not true climax associations, for they will gradually increase in mesophytism until the pioneer plants of the true climax may enter. Such associations should not be classed as "climax associations," but should be distinguished by some other term such as *temporary climax associations.* (Nichols, *l.c.*)

Although Transeau (1905 B, 1906) did not seem to recognize the position of the beech-maple series in the successions of southern Michigan, he described a forest of beech, maple, red oak, white elm, sycamore, basswood, and the like, as typical of the lake-plain. Coons (1911) found maples, elms, basswoods, and others, succeeding pines in the Saginaw region and concluded that the beech-maple type was the climax association. Livingston (1903) gave the beech-maple association as characterizing the heavier clay soils of Kent County, with some hemlock to the northwest. Gates (1912) described the beech-maple-hemlock as the climax for Cheboygan County. In the Northern Peninsula the beech-maple-hemlock was shown to be the climax by Whitford (1901). Ruthven (1905) and Adams (1905 A) found no Fagus in the Porcupine Mountains of the Upper Peninsula, though a climax forest of sugar-maple with a small amount of balsam-fir, basswood, and hemlock occurred there. Isle Royale was shown by Adams and Ruthven and also by Cooper (1913) to be dominated by a climax of spruce, birch, and balsam-fir, the climax for the northeastern conifer province; they noted sugar-maple as dominant on a ridge to the southwest, however, and recorded this as its extreme northern limit in the State.

### B. COMPOSITION OF THE CLIMAX FOREST IN MICHIGAN

The climax forest in the Southern Peninsula of Michigan is a mesophytic forest characterized by deep shade beneath the dominants, and by a ground cover of moist humus. The dominant species are trees, but which of these are the true dominants can be recognized only by comparing their relative frequencies in the single habitats, and their occurrence in the several habitats. In Table I are given the percentage frequencies of some of the trees which commonly occur in this climax association. The percentage frequency was determined for each species by recording the number of times that it was seen within a distance of ten feet on either hand in making a line-transect through the individual association, and then expressing this in percentages in relation to the total number of all species thus noted. In this table not all of the species seen are included, for some were not abundant enough to make up one per cent of the trees, and hence were scarcely important as dominants; others were so typical of a preceding association as to warrant their exclusion. A few such as the white oak are scarcely typical, but occur so often that they were included as indices of the forest type.

As it was not possible to spend an entire summer at each of the stations concerned, the lists of secondary species are not complete; many of the more important secondaries can be recognized, however, at any time of the year, either by foliage, flower or fruit, or, if these be lacking, by remnants of these which often persist the entire winter and even far into the early summer. Quadrat studies for the frequency and abundance of the secondary plants (Clements, 1905) were made for many of the stations, but as they seemed of little value for the wide range of territory studied, they are not taken up in this paper. The secondary plants are of little importance in the association, except as indicators of the degree of dominance of the tree-species. Many are able to grow under any tree-growth as soon as conditions are sufficiently mesophytic, while others are entirely dependent on certain species of trees for their existence

because they are limited to special kinds of humus. The first sort often precedes the climax association, but the second comes in only when conditions have become relatively stable as regards the dominance of the trees of the climax association.

*Dominant Species*

The dominant species in the climax association are the trees listed as follows: *Acer saccharum*, *Betula lutea*, *Carya cordiformis*, *Fagus grandifolia*, *Fraxinus americana*, *Ostrya virginiana*, *Quercus rubra*, *Tilia americana*, and *Ulmus americana*. They are dominant by size and shading, interference with air-movement or wind-protection, and by humus formed from the fallen individuals or parts. Of these trees maples and beech make up about sixty per cent on the average, and the others mentioned make up about thirty per cent; the remaining ten per cent is made up by many different species of trees which vary in kind in the different parts of the State (See Table I). These less important trees are represented in the southern part of the State by *Liriodendron Tulipifera*, *Nyssa sylvatica*, *Platanus occidentalis*, *Prunus serotina*, *Quercus bicolor*, and *Sassafras variifolium*, and in the north by *Prunus pennsylvanica* and *Tsuga canadensis*.

*Acer saccharum*, the sugar-maple, is almost invariably present in the climax association as an important dominant. Although it is more frequent on clay soils, it is found on both clay and sand, the ratio of occurrence being about 2 : 1. The climax is reached more quickly on clay than on sand and this explains the present greater frequency on clay.

*Betula lutea*, the yellow birch, is frequently found in the association in the northern part of the State. Its distribution in the southern part is more scattered, but it may be found in every region of the Lower Peninsula.

*Carya cordiformis*, the bitternut hickory, occurs frequently in the southern consocies in this State, but is of general distribution as it occurs to some extent in the north also.

*Fagus grandifolia*, the American beech, is a most characteristic dominant of the beech-and-maple climax association. It is found most frequently on clay soils, but wherever sand has

had a sufficiently long development of humus, and where soil-water is not too inadequate, beech will develop with the other trees of the climax forest. The beech is considered by some to be an obligative mycorrhizal plant. If this be true, it will explain its restriction to good humus with plenty of soil-water

TABLE I

PERCENTAGE FREQUENCIES OF TREES IN THE CLIMAX ASSOCIATION OF SOUTHERN MICHIGAN

| | Acer saccharum | Fagus grandifolia | Tilia americana | Ulmus americana | Fraxinus americana | Ostrya virginiana | Quercus rubra | Carya ovata | Prunus serotina | Carya cordiformis | Juglans cinerea | Quercus alba | Tsuga canadensis | Liriodendron tulipifera | Betula lutea | Other trees |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| REGION I | | | | | | | | | | | | | | | | |
| Richmond | 22 | 20 | 5 | 12 | 9 | 11 | 2 | 4 | .. | 1 | 1 | 1 | .. | 1 | 6 | 5 |
| Wayne | 9 | 22 | 2 | 6 | 6 | .. | 8 | 2 | .. | 2 | .. | 5 | .. | 1 | .. | 37 |
| REGION II | | | | | | | | | | | | | | | | |
| Clayton | 53 | 18 | 2 | 6 | 6 | 1 | 1 | 3 | 2 | 1 | .. | .. | .. | .. | .. | 7 |
| Ann Arbor | 8 | 9 | 17 | .. | 14 | 7 | 4 | 1 | 1 | .. | .. | .. | .. | .. | .. | 39 |
| Charlotte | 20 | 52 | 2 | 6 | 4 | 3 | 2 | .. | 4 | 6 | 1 | .. | .. | .. | .. | .. |
| Davison | 23 | 41 | 8 | 5 | 3 | 8 | 4 | 3 | .. | .. | .. | .. | .. | .. | .. | 5 |
| Clifford | 48 | 19 | 6 | 13 | 3 | 5 | .. | .. | 1 | .. | .. | .. | 1 | .. | .. | 4 |
| REGION III | | | | | | | | | | | | | | | | |
| Coldwater | 45 | 39 | 3 | 3 | .. | 7 | .. | .. | .. | .. | 2 | .. | .. | .. | .. | 1 |
| Bronson | 60 | 5 | 5 | 6 | 2 | .. | 4 | .. | 4 | 2 | 5 | 2 | .. | 2 | .. | 3 |
| Berrien Springs | 38 | 29 | 12 | 6 | 5 | 1 | 2 | .. | 1 | 1 | .. | 1 | .. | 2 | .. | 2 |
| REGION IV | | | | | | | | | | | | | | | | |
| Moseley | 24 | 43 | 13 | 2 | 4 | 2 | 3 | 3 | 1 | .. | 2 | 2 | .. | 2 | .. | .. |
| Clare | 9 | 65 | 2 | 1 | 4 | 1 | 4 | .. | .. | .. | .. | .. | 12 | .. | .. | 2 |
| Hart | 26 | 36 | 1 | 5 | 2 | 1 | .. | .. | 9 | .. | .. | .. | 18 | .. | 1 | 1 |
| REGION V | | | | | | | | | | | | | | | | |
| Vassar | 23 | 68 | 2 | .. | .. | .. | .. | .. | .. | .. | .. | 2 | .. | .. | .. | 5 |
| Pigeon | 8 | 12 | 4 | 36 | .. | .. | 1 | 2 | .. | .. | 3 | .. | .. | .. | 4 | 30 |
| REGION VI | | | | | | | | | | | | | | | | |
| La Rocque | 40 | 49 | 1 | 1 | .. | 1 | .. | .. | .. | .. | .. | .. | 7 | .. | 1 | .. |
| Douglas Lake | 35 | 48 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 17 | .. | .. | .. |

in regions where it is otherwise absent. The ratio of occurrence on sand and clay is about 1 : 2. Its distribution is general throughout the Lower Peninsula.

*Fraxinus americana*, the white ash, occurs indiscriminately on sand or clay throughout the Lower Peninsula, although it is less frequent towards the north where it is often replaced by *F. nigra*.

*Ostrya virginiana*, the hop hornbeam, occurs very generally in the State, but is more abundant in the southern consocies of the association.

*Quercus rubra*, the red oak, is often present in this association, especially in the southern part of the State. It is also a member of the oak-hickory association and occurs in the climax when it is on dry or "light" soils.

*Tilia americana*, the basswood, is a frequent member of this association and occurs throughout the peninsula, but more frequently on clay soils in the southern part.

*Ulmus americana*, the white elm, is a member of the climax association throughout the Lower Peninsula, especially in the southern part. Its ratio of occurrence on sand and clay is 3:5 Next to the sugar-maple it is the most common member of this association.

*Liriodendron Tulipifera*, the tulip-tree, is not very abundant in any part of the State, but is most frequent in the southwest corner, where it is an important member of the association. On the western side of the peninsula it extends as far as a few miles north of the Grand River.

*Nyssa sylvatica*, the sour gum, is never an important tree in this association either as regards size or numbers. It is often present in the southern part of the State.

*Platanus occidentalis*, the sycamore, extends north of the Grand River as far as Sparta and Smyrna, both being not more than five miles north of the Grand River Valley. It is more frequently seen on sand, being prevalent in the river valleys. In the southwest and southeast parts of the State it is often seen in the climax association.

*Prunus serotina*, wild black cherry, is seen in most of the consocies of this association in the Lower Peninsula, but is not abundant in the northern ones. It grows to be a large tree, sometimes almost losing its distinctive bark character in age. In the north it is replaced by *Prunus pennsylvanica*.

*Sassafras variifolium*, sassafras, occurs as a shrub and as a tree very sparsely in the climax association. It is more characteristic in the oak-hickory association, and occurs in the stages of

succession of this association by the climax when the sugar-maple is present and is beginning to succeed the oaks. It was not seen in the northern part of the peninsula, but occurred as far north as White Cloud, forty miles north of the Grand River, and near Lake Michigan it was seen twenty miles north of Grand Haven.

*Tsuga canadensis*, the hemlock, occurs in the northern consocies, but extends south on both sides of the peninsula. Along Lake Michigan it is found as far south as the state-line between Michigan and Indiana; along Lake Huron it occurs as far south as Jeddo, not far from Port Huron, where it was seen on till-clay.

### *Shrub Zone*

The shrub zone is variable in composition, in general being made up of young trees of the dominant species. The following are also characteristic of the shrub zone in the Lower Peninsula: *Amelanchier canadensis*, *Carpinus caroliniana*, *Ribes Cynosbati*, *Rubus allegheniensis*, *R. idaeus*, *R. idaeus aculeatissimus*, *Sambucus canadensis*, *Viburnum acerifolium*, and *Zanthoxylum americanum*.

Southern shrubs which enter the peninsula, but do not occur throughout are: *Aesculus glabra*, *Asimina triloba*, *Benzoin aestivale*, *Cornus alternifolia*, *C. paniculata*, *C. stolonifera*, *Corylus americana*, *Crataegus spp.*, *Morus rubra*, *Rosa humilis*, *Staphylea trifolia*. Those present in the north, but seldom or never seen in the southern part of the peninsula, are: *Acer pennsylvanicum*, *A. spicatum*, *Gaylussacia baccata*, *Rosa blanda*, *Sambucus racemosa*, and *Taxus canadensis*.

*Rhus Toxicodendron* is the only liana of nearly universal distribution in the Lower Peninsula. *Celastrus scandens*, *Clematis spp.*, *Dioscorea villosa*, *Smilax herbacea*, *S. hispida*, and *Vitis cordifolia* are southern, while *Lonicera canadensis* is northern, in distribution.

### *Secondary Plants*

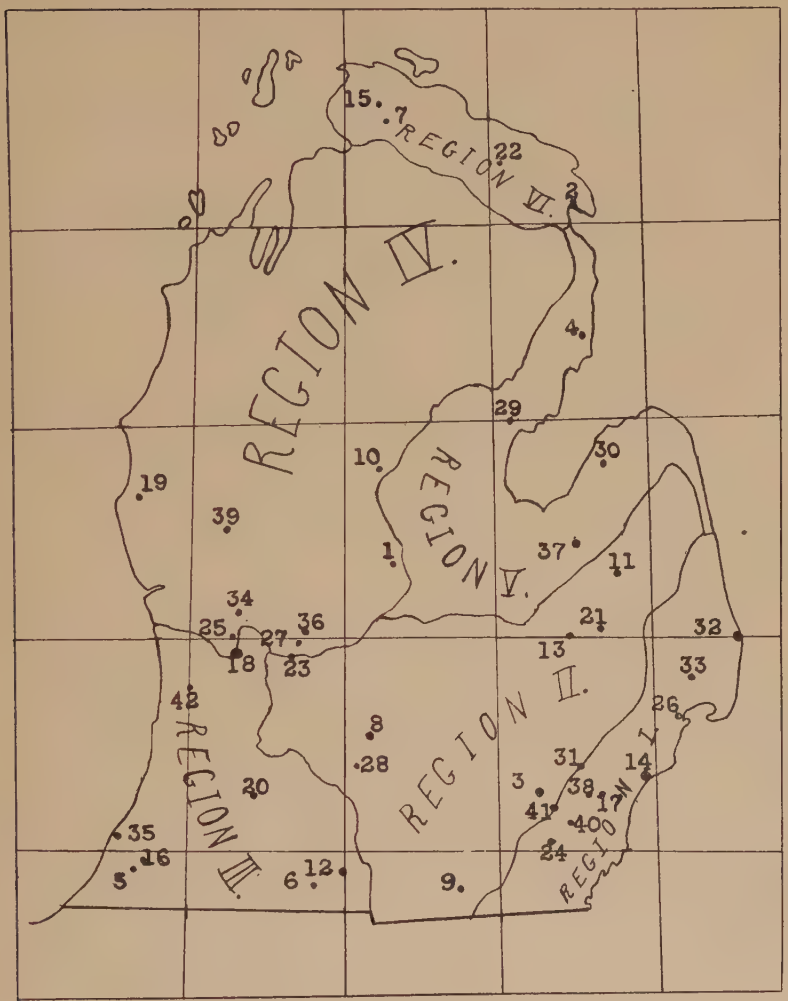
The secondary plants are mostly herbaceous, and, because of the lack of light, are not numerous in any of the patches of climax association. A large number of species occur in such

situations, but they vary from place to place. Those secondary plants showing the greatest frequency in the climax association and seldom found elsewhere are: *Actaea alba, Adiantum pedatum, Allium spp., Apios tuberosa, Asplenium felix-foemina, Aralia racemosa, Arisaema triphyllum, Aspidium Goldianum, A. spinulosum, A. noveboracense, Botrychium virginianum, Carex plantaginea, C. tribuloides, Circaea alpina, Corallorhiza maculata, Cypripedium parviflorum* var. *pubescens, Cystopteris bulbifera, C. fragilis, Epifagus virginiana, Galium circaezans, G. tinctorium, Geranium Robertianum, Hystrix patula, Maianthemum canadense, Medeola virginiana, Mitella diphylla, Monotropa uniflora, Onoclea sensibilis, O. Struthiopteris, Osmorhiza longistylis, Osmunda cinnamomea, O. Claytoniana, Phegopteris Dryopteris, P. hexagonaptera, Podophyllum peltatum, Polygonatum biflorum, Polystichum acrostichoides, Smilacina racemosa, Thalictrum dioica, Trillium grandiflorum, Viola papilionacea,* and *Viola pubescens.*

Other secondary plants which are often found are not as typical. Of these *Aralia nudicaulis* is often present, but occurs also in the oak-hickory association, as does also *Mitchella repens.* Those occurring only in the southern consocies are: *Anemonella thalictroides, Asarum canadense, Carex conjuncta, C. filiformis, C. lupuliformis, C. lupulina, C. pennsylvanica, Erythronium albidum, E. americanum, Evonymus obovatus, Hydrastis canadensis, Laportea canadensis, Menispermum canadense, Phryma Leptostachya, Rhus canadensis, Trillium declinatum, Uvularia perfoliata, Viola canadensis, V. hastata, V. palmata, V. sororia,* and *V. striata.* Other secondary plants which are mostly northern in distribution are: *Actaea rubra, Botrychium ternatum, Clintonia borealis, Cornus canadensis, Gaultheria procumbens, Habenaria orbiculata, Linnaea borealis* var. *americana, Lycopodium annotinum, Mitella nuda, Pyrola asarifolia, P. elliptica, Smilacina stellata, Streptopus roseus,* and *Trillium cernuum.*

### C. DISTRIBUTION OF THE CLIMAX FOREST IN MICHIGAN

The Lower Peninsula was divided, for convenience of study, into six regions which are separated from one another to some




MAP II. Regions of the Southern Peninsula of Michigan

The numbers on the map refer to some of the principal localities mentioned in the text: 1. Alma; 2. Alpena; 3. Ann Arbor; 4. Au Sable; 5. Berrien Springs; 6. Bronson; 7. Burt Lake; 8. Charlotte; 9. Clayton; 10. Clare; 11. Clifford; 12. Coldwater; 13. Davison; 14. Detroit; 15. Douglas Lake; 16. Eau Claire; 17. Eloise; 18. Grand Rapids; 19. Hart; 20. Kalamazoo; 21. Lapeer; 22. La Rocque; 23. Lowell; 24. Milan; 25. Mill Creek; 26. Mt. Clemens; 27. Moseley; 28 Olivet; 29. Omer; 30. Pigeon; 31. Plymouth; 32. Pt. Huron; 33. Richmond; 34. Sparta; 35. St. Joseph; 36. Smyrna; 37. Vassar; 38. Wayne; 39. White Cloud; 40. Willis; 41. Ypsilanti; 42. Zeeland.

extent by natural barriers; these are shown in Map II. In each of these regions a large number of stations were visited, but as space will not allow a detailed description of each station, they will be referred to only where they mark the limits of distribution of individual species.

*Region I. The Southeastern Lake Plain*

This region lies along the shore of Lake Erie and the Detroit River from the Ohio line as far north as Port Huron, extending back inland as far as the morainal ridges which parallel the lake margin at a distance of about twenty-five miles.

It is characterized by soils of lake origin, mostly lake clays and lake sands laid down in the glacial period. The soils best suited for the development of the climax in this region were somewhat "heavy" clays. The forests are dense and the shrubs and lianas not abundant, being usually limited to marginal zones. The soils are much modified by humus, and water relations are more toward the hydrophytic than the xerophytic extreme.

The dominants were much the same as those for the entire peninsula, being *Acer saccharum*, *Fagus grandifolia*, *Fraxinus americana*, *Tilia americana*, and *Ulmus americana*. *Betula lutea* was found at Richmond and *B. alba* at Mt. Clemens, both in the northeastern part of the region; *Liriodendron* was frequent throughout. *Acer rubrum*, *A. saccharinum*, *Celtis occidentalis*, *Fraxinus nigra*, *F. pennsylvanica* and *Nyssa sylvatica* were occasionally found in lowland habitats, while *Carya ovata*, *Juglans cinerea*, *Quercus alba*, *Q. macrocarpa*, *Q. rubra*, and *Sassafras variifolium* were often present in the upland habitats as relicts of the preceding oak-hickory association.

The shrub zone is made up of young trees of beech, tuliptree, hornbeam and cherry (*Prunus serotina*), and often of young oaks, hickories and sassafras where some interference has made light conditions favorable to these. *Sambucus canadensis* is the most abundant shrub, and besides those which are general in distribution, *Gaylussacia baccata* and *Vaccinium canadense*, which are mainly northern, occur here as far south as Willis.

The secondaries are in general those listed as "general" or "southern." The most frequent secondaries were *Evonymus obovatus* and *Smilacina racemosa*, which were found nearly everywhere. *Aralia nudicaulis*, *Aspidium noveboracense*, *Asplenium felix-foemina*, *Chimaphila umbellata*, *Cypripedium parviflorum* var. *pubescens*, *Medeola virginiana*, were not observed in any of the stations, although they occur in other southern regions. Plants scarce in the south were: *Aspidium Goldianum*, at Quirk's Woods south of Ypsilanti; *Gaultheria procumbens* at Wayne, and at Eloise; and *Smilacina racemosa* at Willis and at Milan.

### *Region II. The Inland Morainic Region*

This region is made up of clay and sand moraines. It is located west of Region I and extends north to the Grand and Maple rivers, and west to the Looking-glass River along which the western boundary turns south to the state line (See Map II). The climax forest occupies both lowland soils and upland soils of lighter nature. The forests are generally dense and shady but with more undergrowth, the shrub zone being not limited to a marginal zone, but also present as a poorly developed layer within the forest. (See Plate XX, Fig. 1.)

The most abundant dominants for the region are: *Acer saccharum*, *Fagus grandifolia*, *Fraxinus americana*, *Ostrya virginiana*, *Prunus serotina*, *Tilia americana*, and *Ulmus americana*. In the lowlands *Acer rubrum*, *A. saccharinum*, *Betula lenta*, *Fraxinus nigra*, *F. pennsylvanica*, *Nyssa sylvatica*, *Quercus bicolor*, and *Ulmus fulva* occur also; *Juglans cinerea*, *J. nigra*, *Liriodendron Tulipifera* and *Quercus Muhlenbergii* occur in drier situations.

The shrub zone is composed of young trees of hickory, hop-hornbeam, wild cherry, red oak, sassafras and elm, and all of the shrubs of general and southern distribution for the State (excepting *Aesculus glabra*) and with the addition of *Corylus americana*, *Hamamelis virginiana*, *Rhus glabra*, and *R. typhina*, which abound here as well as in the north. *Sambucus racemosa* occurs here at Clifford in the northeastern part of the region.

Most of the secondaries are those listed as general or southern in the State. The following northern species were also present: *Asplenium felix-foemina* at Third Woods near Ann Arbor, *Medeola virginiana* near Lapeer, and *Mitchella repens* at Olivet. The following species, although probably occurring in other stations in this region, were not seen in any of those visited: *Aralia racemosa*, *Arisaema triphyllum*, *Aspidium Goldianum*, *Chimaphila umbellata*, and *Menispermum canadense*.

### *Region III. The Southwestern Outwash Region*

This region is composed of soils similar to those of Region II, but more mixed with glacial outwash of both sand and clay. It comprises all of the west side of the State south of the Grand River Valley. The climax forest occurred on several soil types, sometimes well drained but with good humus. The shade is dense, but the shrubs occur in from one to three well-defined layers or stories under the dominants.

The most abundant dominants are: *Acer saccharum*, *Carya cordiformis*, *Fagus grandifolia*, *Fraxinus americana*, *Juglans cinerea*, *Liriodendron Tulipifera*, *Ostrya virginiana*, *Platanus occidentalis*, *Tilia americana*, and *Ulmus americana*. *Betula lutea* was not seen in any of the stations, and *Celtis occidentalis*, *Fraxinus quadrangulata*, *Juglans nigra*, *Prunus serotina*, *Quercus rubra*, and *Sassafras variifolium* were only occasionally found in the climax association here.

The shrub zone contains young trees of sugar-maple, bitternut, beech, tulip-tree, and sassafras in abundance, and all of the shrubs listed for general and southern distribution including *Aesculus glabra*, which was found frequently near Berrien Springs.

Of the secondaries of general distribution, *Actaea alba* occurred at Berrien Springs, though it is scarce in the southern part of the State. *Aralia racemosa*, *Aspidium Goldianum*, *Asplenium felix-foemina*, *Chimaphila umbellata*, *Cypripedium parviflorum* var. *pubescens*, *Medeola virginiana*, and *Onoclea Struthiopteris* were not seen in any of the stations. Most of

the southern species were seen with the exception of *Erythronium albidum*, *E. americanum*, *Laportea canadensis*, and *Uvularia perfoliata*. Of the northern species *Gaultheria procumbens* comes as far south as ten miles south of Zeeland.

### *Region IV. The Northern Morainal Region*

This region is a large one as the study was made more especially for the southern part of the peninsula, and the stations of this and the two following regions were studied merely for comparison. This region occupies all of the western and central part of the peninsula north of the Grand River. Its soils are varied, being morainal sands and clays, outwash sands and clays, and a very small proportion of lake sands and clays especially dunes in the western shore region. The climax forest here occupies both high and well-drained soils and low boggy soils. In both situations it is dense and has much humus.

The most important dominants for this region are: *Acer saccharum*, *Betula lutea*, *Carya cordiformis*, *Fagus grandifolia*, *Fraxinus americana*, *Ostrya virginiana*, *Quercus rubra*, *Tilia americana*, *Tsuga canadensis*, and *Ulmus americana*. Near Alma and Clare *Betula alba* is often present in the climax; *Pinus Strobus* and *Larix laricina* often occur as relicts of past associations. In the southern border of the region some species of more southern range occur, as *Juglans cinerea* at Moseley and Alma, tulip-tree at Mill Creek and at Moseley, *Platanus occidentalis* at Mill Creek, and *Ulmus racemosa* at Hart.

The shrub zone contains those species listed for northern and general distribution as well as young trees of maple, bitternut, beech, hop-hornbeam, wild cherry, red oak, sassafras, and elm. At Moseley *Liriodendron Tulipifera* was found reproducing abundantly, so that young trees of this species made up a considerable part of the shrub zone, disproving Beal's statement (1904) that it is never found north of the Grand River Valley. *Zanthoxylum americanum* occurs as far north as Smyrna.

The secondary plants are those characteristic of the northern part of the State, with those of general distribution. A few

southern plants cross the barrier of the Grand River Valley, *Caulophyllum thalictroides* being seen at Alma and at Hart, *Evonymus obovatus* at Alma and at Clare, *Laportea canadensis* at Alma and at Moseley, *Phryma Leptostachya* at Alma and at Moseley, and *Uvularia perfoliata* at Hart.

### *Region V. The Saginaw Bay Region*

The soils of this region are similar to those of Region I, being mostly lake sands and clays laid down in various ways. The region occupies the lands adjacent to Saginaw Bay to about twenty-five miles inland. Here the climax forest is characteristic as regards its secondary plants only on clay soils, but when present on sand a layer of humus covers the sandy surface.

The dominants are: *Acer saccharum*, *Betula lutea*, *Fagus grandifolia*, *Fraxinus americana*, *Tilia americana*, *Tsuga canadensis*, and *Ulmus americana*. The bitternut is only occasionally present, as are also *Fraxinus nigra* and *F. pennsylvanica*. As relicts from hydrarch successions *Acer rubrum* and *A. saccharinum* are often present, while *Carya ovata*, *Pinus Strobus*, *Populus grandifolia*, *P. tremuloides*, and *Quercus alba* are often relicts of the xerarch successions. *Juglans cinerea* is rare, being seen no farther north than Lapeer; *Platanus occidentalis* was seen at Vassar.

The shrub zone includes *Alnus incana* and *Corylus americana* as well as the shrubs listed for general distribution; northern shrubs present were *Acer spicatum*, *Gaylussacia baccata*, and *Rosa blanda*.

Secondary plants were nowhere abundant. The only secondaries of general distribution which were at all frequent were: *Adiantum pedatum*, *Apios tuberosa*, *Aspidium spinulosum*, *Chimaphila umbellata*, *Circaea alpina*, *Corallorhiza maculata*, *Cypripedium parviflorum* var. *pubescens*, *Epifagus virginiana*, *Mitchella repens*, *Osmunda cinnamomea*, *O. Claytoniana*, *Podophyllum peltatum*, *Viola papilionacea*, and *V. pubescens*. Secondary plants of northern distribution found here were: *Botrychium ternatum* var. *intermedium*, and *Gaultheria procumbens*. Southern species found here were *Arisaema triphyllum*, *Laportea canaden-*

*sis*, and *Rhus canadensis* at Pigeon, and *Evonymus obovatus* at both Pigeon and Vassar.

### *Region VI. The Northern Shore Region*

In this region the soils are of all sorts, having clay and sand of all types. The region includes the tip of the peninsula from Little Traverse Bay to a point south of Alpena, and is a strip about twenty-five miles wide. The climax forest grows on all types of soil except bogs. Even on sand it has a well-developed humus layer, and in its dense shade a surprising variety of secondary plants are able to flourish.

The dominants are: *Acer saccharum, Betula lutea, Fagus grandifolia, Fraxinus nigra, Ostrya virginiana, Tilia americana,* and *Tsuga canadensis. Fraxinus americana* is only occasionally present, as is also *Prunus pennsylvanica; Tilia americana* is rare, probably reaching its northern limit in this region near La Rocque. (See Plate XX, Figs. 2 and 3.)

The shrubs are those listed as northern: *Acer spicatum, A. pennsylvanicum, Rosa blanda, Sambucus racemosa, Taxus canadensis,* and *Vaccinium canadense.* Those of more general distribution occurring here are: *Amelanchier canadensis, Carpinus caroliniana, Rubus allegheniensis, R. idaeus, R. idaeus* var. *aculeatissimus, Sambucus canadensis.* None of the species listed as southern occur here. *Rhus Toxicodendron* does not occur here as a liana in the forest, but is a shrubby plant which grows erect along sandy shores, and on dunes, so it is seldom found in this association.

The secondary plants include most of those listed as general or northern, but *Apios tuberosa* and *Mitella diphylla* were not seen in the region. The yellow ladies'-slipper here is confined to bogs, and *Gaultheria procumbens* prefers the pine association. *Trientalis americana* was present in the climax forests of this region, though not seen in the stations of any other region; *Habenaria orbiculata* occurred in Bryant's woods near Douglas Lake. *Viola palmata* was found in one station of this region, near La Rocque.

## D. THE CAUSES OF THE PRESENT DISTRIBUTION

### *Climatic Factors*

Neither the "isoatmic" lines of Livingston (1911) nor the temperature summations or "efficiencies" (Livingston and Livingston, 1913) are of value in explaining the distribution of plants within the State. The ratios of evaporation to rainfall (Transeau, 1905) are somewhat better, but they do not mark out the actual areas of distribution. That the relation is not merely one of rainfall is seen by examining such a map as that by Gannett (1909), which shows the amount of rainfall for the State. Drude (1890) shows a map of the floral regions based on the duration of the cold and warm months, and the line in Michigan which divides the southern part having a hot summer from the northern part having a moderate summer and a cold winter coincides much better with the southward extensions of the northern plants in the State.

The northern boundary for southern species in the State forms a V-shaped figure and the southern boundary for northern species forms an inverted V, as has been already mentioned by many writers concerning the vegetation of lower Michigan. The northern as well as the southern species are distributed farther from their centers of greatest abundance along both lakes, so that for either northern or southern species the boundary line curves either to the north or to the south in the central part of the peninsula. The more moderate climate of the lake shores allows the northern plants to remain here uninjured by the heat of the summer, and at the same time allows a northward advance of southern species in the same regions because of the lessened severity of the winter.

### *Edaphic Factors*

1. *The chemical nature of the soil.* — The majority of the soil-studies that have been made, especially those dealing with botanical investigation, have been made with reference to the water-content of the soils. Some good work has been done on

the chemical nature of the soils; the work of Dachnowski on the effect of dissolved substances in the soil-water is one of these. Hollick (1880) and Evans (1889) classified plants according to the geological formations on which they occurred, and in Europe it has been customary to classify plants as to their soils, as in Tansley's *Types of British Vegetation* (1911).

The relation of vegetation to the chemical nature of the soil may be shown by the study of the soil analyses made by Kedzie (1893). As the forest-type was noted for many of his samples, it has been possible to combine his data into the following table in which twelve beech-supporting soils are compared with six pine-supporting soils.

TABLE II

Comparison of Beech- and Pine-supporting Soils

| | Soils with beech | | | Soils with pine | | |
|---|---|---|---|---|---|---|
| | Low | High | Average | Low | High | Average |
| Silicon | 65.48 | 91.92 | 77.45 | 75.74 | 95.02 | 90.63 |
| Aluminum | 2.86 | 15.60 | 6.40 | 0.49 | 10.63 | 2.98 |
| Iron | 0.90 | 7.91 | 4.10 | 0.78 | 3.80 | 1.60 |
| Calcium | 0.40 | 1.64 | 1.11 | 0.20 | 0.94 | 0.41 |
| Magnesium | 0.13 | 1.23 | 0.60 | 0.12 | 0.48 | 0.22 |
| Potassium | 0.61 | 2.12 | 1.40 | 0.20 | 1.96 | 0.67 |
| Sodium | 0.28 | 1.20 | 0.76 | 0.26 | 1.25 | 0.72 |
| Sulfate | 0.10 | 0.30 | 0.21 | 0.05 | 0.26 | 0.10 |
| Phosphate | 0.13 | 0.49 | 0.30 | 0.01 | 0.44 | 0.14 |
| Organic matter | 2.05 | 7.48 | 3.90 | 1.34 | 2.97 | 2.13 |
| Water | 0.35 | 4.00 | 1.63 | 0.20 | 1.44 | 0.49 |

The amount of silica appears important, as the averages differ thirteen per cent; but while the five samples lowest in silica supported beech, and the four highest in silica supported pine, those between were beech-supporting on the ones having the higher silica content! The aluminum salts present indicated the amount of clay mixed with the sand, and although the four lowest in aluminum supported pine, the other pine soils con-

tained more aluminum than six of those supporting beech! Calcium has been supposed important for beech, but four of the beech-supporting soils were as low in calcium content as the highest of the pine soils, or even lower. Harper (1913) considered potassium more important than calcium for beech, but it was more abundant in two of the pine-soils than in six of the beech-soils; the four soils lowest in potassium were, however, pine-supporting.

There is seen in these samples a general tendency for soils higher in amounts of mineral nutrients to support a mesophytic forest, while those containing a higher proportion of silica support a xerophytic forest-type. Half of the samples could have supported either forest-type, as far as the mineral constituents were concerned. The original condition of the soil is not important as long as there are no harmful salts present, for it becomes richer as time goes on by the action of the vegetation.

The various stations studied were situated on soils of all kinds. A few examples will show the varied character of these soils. In Region I climax forest was present on lake clay (Milan, Plymouth, Quirk's Woods), on lake sand (Wayne, Willis, Richmond), and on morainal clay (Mt. Clemens). In Region II it was present on outwash sand (South Main St. woods near Ann Arbor), on morainal sand (Olivet), on till-clay (Third Woods near Ann Arbor, Davison, Charlotte), on morainal clay (Ypsilanti, Clayton, Lapeer, Clifford). In Region III the climax occurred on outwash sand (Kalamazoo), on outwash clay (Coldwater), on till-clay (Bronson, Eau Claire), and on morainal clay (Berrien Springs). In Region IV it was found on morainal sand (Mill Creek, Lowell, Hart), on till-clay (Moseley, Clare), and on morainal clay (Alma). In Region V it occurred on lake sand (Au Sable), on lake clay (Pigeon, Omer), and on morainal clay (Vassar). In Region VI it was present on outwash sands (Burt Lake), on morainal sand (La Rocque) and on morainal clay (La Rocque, Douglas Lake). The present distribution disproves, therefore, any statements as to chemical limitations based on the inorganic soil-constituents.

2. *Organic material, or humus.* — The analyses made by

Kedzie showed that the organic matter in beech-supporting soils is much greater than in pine-supporting soils. The presence of humus increases the amount of nitrogen present both directly in the nitrogen compounds of the fallen plant-parts and in the harboring of organisms which may be useful in fixing nitrogen. Humus increases the water-content by preventing surface-evaporation and by providing a spongy layer to absorb water and thus cut down surface run-off. Humus harbors many saprophytic bacteria and fungi which are of great value in changing the chemical and physical nature of the soil, and in some cases some of these are present on the roots of the trees in "mycorrhizas" which may be of benefit. Inorganic salts which have been brought to the plants from far beneath the surface by the roots are added to the surface soil by the fallen vegetative parts. It will thus be evident that the organic matter of the soil is of great importance as regards the mineral content of the surface soil, the water-content, nitrogen content, and biotic factors of the soil.

3. *Water-relations of the soil.* — The climax association occurs on soils which vary greatly in water-content. Conditions which are originally much too dry are made endurable for the climax forest by the development of a humus layer. On the other hand, conditions of saturation by water are remedied by the development of humus by other associations, and when the surface layers become sufficiently aerated, the climax can develop. The preponderance of the climax association on clay soils is because of the combination of water-relation and humus factors; these are mutually interdependent. Where water is present in sufficient amount, as is usually true of clay soils, humus develops quickly. Where water conditions are less favorable humus develops more slowly, but will in time so change the water-relations that the soil will become usable for the climax association. Wherever sand is sufficiently moist, humus develops and the climax is finally reached, and here, too, humus develops less rapidly on dry soils, but will in time accumulate so that the climax may develop. The difference between the availability of clay and sandy soils is mainly one of

time; in the case of sand a relatively longer time must elapse before a soil is fitted for the climax association.

*Historical Factors*

It is probable that one of the best explanations of the present distribution of the climax association is the relation to past conditions. The lack of northern forms in the south-central part of the peninsula is to be explained by the theory of Transeau (1903), that the land south of Michigan in Ohio and Indiana was never occupied by conifers, but that the deciduous trees followed the ice-retreat directly in this part of the State. It is probable that the majority of the plants entered the State from the southwest and southeast corners, and this would explain the farther penetration along the sides by so many species. The fact that the climax association of the southwest corner is of a high type, and occurs on sandy as well as on clay soils, indicates an entrance at this corner by many of the species, probably preceding the "xerothermic period," [2] which ushered in the prairies of the southern part. It is probable that the climax association was present here in some places while the eastern corner was still under glacial waters.

### E. FUTURE OF THE CLIMAX ASSOCIATION

The climax association does not occupy all of the available soils of the State at present. The amounts of nutrients in any soil are probably sufficient for plant growth, and wherever water and humus conditions are favorable, plant-growth will be present, and in time that plant-growth will be replaced by the climax association, provided the natural successions be undisturbed by fire or by man. In a few cases base-leveling must occur before the climax can develop. That there is now a tendency for the climax association to advance northwards is shown by the occurrence of maple forests on Isle Royale in Lake Superior. This advance is more gradual than any taking

[2] Adams, 1910; Alden, 1910; Brock, 1910; Coleman, 1910; Mathew, 1910; and Schulz, 1904, 1907, and 1908.

place in the Lower Peninsula, for the component species of the association are here near the edges of their ranges. In its northern outposts the advance of the association marks the advance of the province of which it is characteristic and is limited by climatic factors; within the province the advance upon other associations is limited only by edaphic factors, the majority of which are either biotic or are due to the previous action of biotic factors. The future of the association, therefore, depends first on non-interference, or rather protection, by man; and after that on the time element alone, for it is capable of occupying all of the soils of the State in time.

## IV. Conclusions

1. The beech-and-maple climax association is an ecological unit for the southern peninsula of Michigan. The differences which occur between the climax forests of the northern and southern portions of the peninsula are not sufficient to warrant the division into two areas each having a different climax.

2. The differences in composition between the northern and southern consocies of the beech-and-maple climax association are due to the limits of distribution of certain of the component species.

3. The present climatic conditions fail to explain the present distribution of many of the component species of the climax association, as many of them are now migrating northward. *Liriodendron Tulipifera* is now extending its range to the north of the Grand River Valley, and is reproducing freely in the most northern station where it was seen.

4. The inorganic constituents of the soil do not act as limiting factors for the climax association. Although the climax association is usually found on clay soils rich in mineral salts, it occurs on all types of soil in all of the regions of the peninsula.

5. The organic matter of the soil is an important factor in determining the development of the climax association. Humus changes the physical composition of the soil, favors the development of soil organisms which may form mycorrhizas with the

roots of some of the higher plants, or may increase or render available the nitrogen supply, and also increases the inorganic constituents of the upper soil layers by the fallen plant parts which have derived these salts through the action of deeply penetrating roots from deeper layers. Wherever the climax association was found, a good humus layer was developed.

6. The water-relations are important only in the earlier stages of development of the climax association. As the water-retaining qualities of the soil may be increased or diminished by the addition of humus, any soil may in time support the climax association.

7. Historical factors are of great importance in explaining the present distribution of the climax association. The "lagging" of certain species in the central region of the State may be due to their having entered from one or both corners, and to their not having as yet completed their invasion of the central region. Many areas at present unoccupied by the climax association may be occupied in the future, when a sufficient time interval has elapsed for the modification of the present soils.

8. The present discontinuity and sparse distribution are due largely to the action of man. In the days of settling the wild country many regions were completely devastated of their virgin timber and have never recovered. The subsequent erosion of the surface soils has made recovery slower.

9. The beech-and-maple climax association is capable, if left undisturbed, of occupying eventually all of the soils of the Lower Peninsula of Michigan, and of perpetuating itself on them, and hence is a true climax association.

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## EXPLANATION OF PLATE XX

FIG. 1. Beech with Undergrowth of Beech. Third Woods, near Ann Arbor. July, 1914.

FIG. 2. Ground-Cover of Young Maples at La Rocque. August, 1914.

FIG. 3. Trunk of Old Yellow Birch, La Rocque. 1914.

PLATE XX

FIG. 1

FIG. 2

FIG. 3